Paleocadmus, a Nautiloid Cephalopod Radula from the Pennsylvanian Francis Creek Shale of Illinois

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(5 Plates; 1 Text figure)

A SINGLE MOLD of an isolated, folded radula has been found in an ironstone concretion from the Essex Fauna of the Francis Creek Shale at Pit Eleven, southwest of Wilmington, Illinois. The Shale is mid-Pennsylvanian, equivalent in age to the Westphalian C of Europe, about 300 000 000 years old. This is a very rich fossil occurrence, yielding intact crustaceans, holothurians, hatchling fishes and young amphibians as well as impressions of such soft-bodied or delicate animals as insects, medusae, priapulids, polychaete worms and several problematic organisms (RICHARDSON & JOHNSON, 1971). Organism-associated radular impressions occur with numerous chitons (RICHARDSON, 1956), an undescribed blob-like coleoid (unpublished data), and the rare belemnite *Jeletzkya douglassae* Johnson & Richardson, 1968 (unpublished data). The present specimen is the only isolated radular impression yet observed, though more than 2 000 000 concretions from this locality are preserved in private and museum collections. Since only 10% to 25% of opened concretions are retained by amateur collectors and perhaps 4% by professional paleontologists, the rarity of this find is emphasized.

LOCALITY, HORIZON, AND MODE OF PRESERVATION

Ironstone concretions at Pit Eleven, which is located on the Will-Kankakee County line about 80 km south of Chicago, are exposed in a 15 m profile of gray shale that is removed as overburden during open-pit mining for coal. The concretions are picked from spoil heaps, split open in the field, and either retained or discarded. Because of specimen scattering by the mining operation, it is not possible to specify precise spatial and stratigraphic association of the organisms.

It appears that the entire profile was deposited over a term of years rather than millenia or centuries, on the seaward slope of a delta at the northeast point of the Illinois Basin. Such distribution data as are available indicate that there was a variety of microenvironments and habitable niches on the delta slope. Elegantly preserved terrestrial forms (amphibians, arachnids, millipedes, insects), typical of the Braidwood fauna a few kilometers to the north, also occur in Pit Eleven. These occurrences attest to the close proximity of the ancient shore.

Burial was rapid; there is evidence that at least some of the specimens, and perhaps nearly all, were buried alive. Before aerobic decomposition of the animals, the remains were firmly embedded in a fine clayey silt. Before completion of anaerobic decay each specimen was encased in a concretion, formed by deposition of iron carbonate within the pore spaces of the silt. Organic tissues inside the concretions may be represented by a film of carbon or by degradation products that penetrated the matrix immediately adjacent to the impression. Fossils of the latter type stand out as light-colored representa-

tions of the organism during the first three years after opening a concretion, but ultimately oxidize to the same deep iron-oxide color as the background. More details of the preservation are given in Richardson & Johnson (1971).

ACKNOWLEDGMENTS

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METHOD OF STUDY

After initial optical observation showed that this was a radular fragment, the concretion halves were trimmed, mounted on SEM stubs, coated successively with carbon and gold, then studied at various magnifications. Preparation technique was as outlined in Solem (1972). The instrument utilized was a Cambridge S4-10, provided Field Museum of Natural History by a grant from the National Science Foundation, GB-34521. A montage of the high information content area in the upper impression is presented as Figure *1*. An artifact caused by the specimen angle in relation to the electron beam means that if Figure *1* is turned upside down, the image appears to contain elevated cusps rather than impressed pits. Minor electronic alterations on the SEM enable preparing reverse images. Figure *23* represents the upper third of Figure *1*, with the heightened illusion of viewing elevated cusps. Stereo pairs in both normal and reverse image also were prepared and used in the attempted reconstruction of radular teeth. Similar photographs of the lower impression were prepared, but are not published because of lesser information content. Higher magnification observations were made on selected areas of both impressions. The published photographs are keyed to Figure *1* by the axis references.

A reconstruction for several half rows is presented in Figure 25. This drawing is based solely on observations from the fossil itself. It was completed prior to the SEM study of a living *Nautilus* radula. It attempts to show the teeth from a viewpoint vertical to the preservation plane.

Radulae from several prosobranch and extant cephalopod taxa were prepared and studied with the SEM in order to associate the fossil with some molluscan group.

SPECIMEN ORIENTATION

The concretion split essentially horizontally to the plane of the radular membrane, allowing for the slight irregularities in the basal membrane itself. The split was relatively near the base of the teeth, leaving deep impressions on one half of the concretion (Figure *1*) and relatively obscure details (Figures *2, 5, 6, 13*) on the other portion, hereafter referred to as the lower side. In Figure *1* the angle of view is from underneath the cusps with the pointed tips disappearing into the matrix. Right and left sides are functionally correct, but the posterior direction is at the top and the anterior at the bottom of the illustration. The lower side impression essentially reflects the basal membrane contours when stripped of the teeth themselves. Figure *24* shows a radular membrane from an extant carnivorous land snail. In the upper right portion, the structures remaining after accidental removal of the individual teeth are roughly comparable to the few details seen in the upper center of Figure *13*, an equivalent part of the fossil radula.

The entire impression is interpreted as representing the anterior folded segment of a cephalopod radula. The expanded membrane normally found in this area of recent cephalopod radulae (see Solem & Roper, 1975) is present as a vague half circle outline around the impression,

Explanation of Figure *1*

Figure *1*: Upper side impression, holotype of ***Paleocadmus herdinae*** Solem and Richardson, gen. nov., spec. nov. Collection of Jerry Herdina, Berwyn, Illinois. Scale line equals 1 mm.

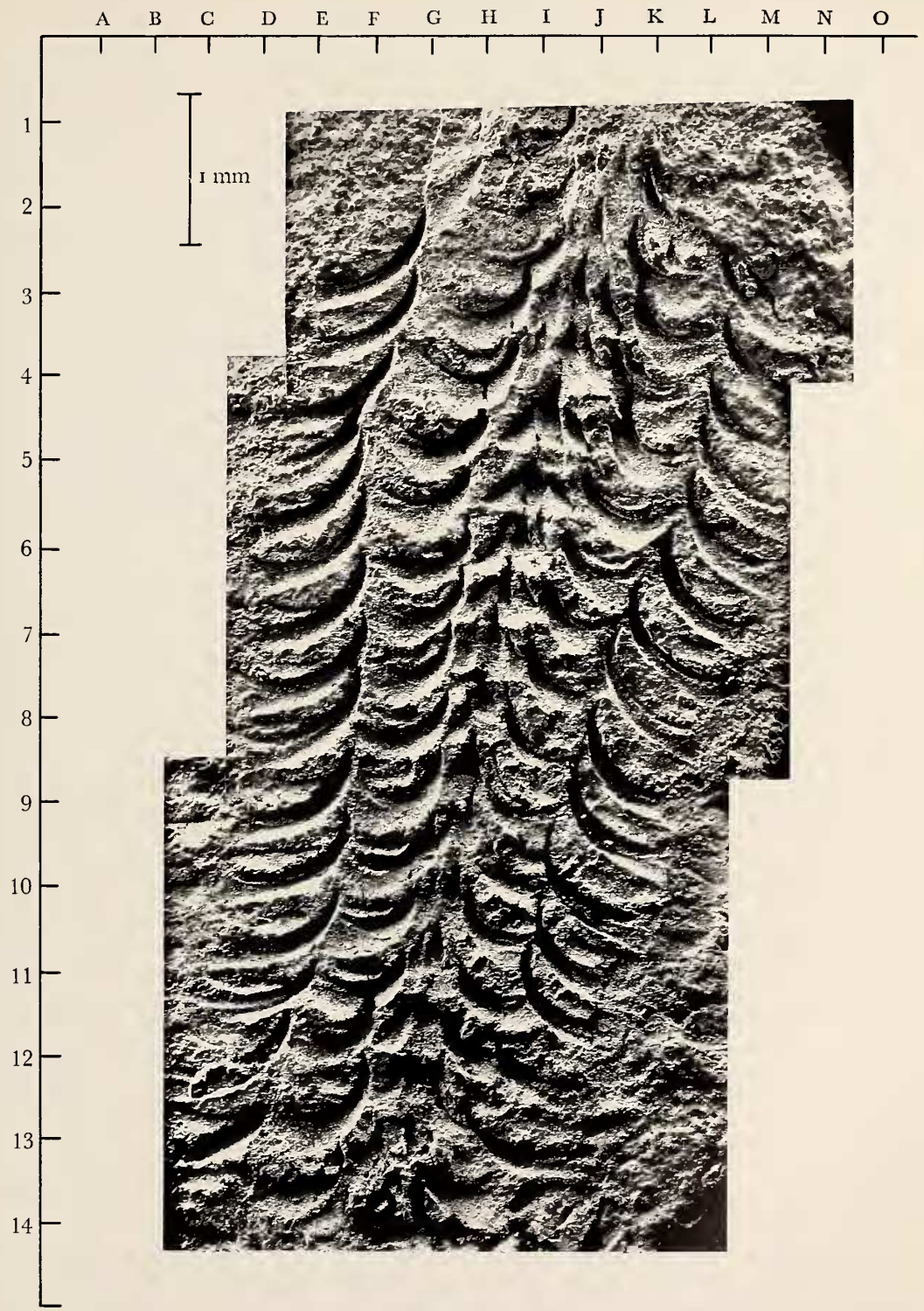

Figure *1*

Upper side impression, holotype of ***Paleocadmus herdinae*** Solem & Richardson, gen. nov., spec. nov. Collection of Jerry Herdina, Berwyn, Illinois

somewhat paler and smoother than the matrix. This "halo" has not been illustrated. The radula was folded under into the lower side of the concretion, with only a small area (Figure *2*) preserved as an open set of tooth impressions. Quite possibly the rest of the radula was torn off prior to preservation. In handling recent cephalopod radulae for comparative studies, there was a distinct tendency for breakage to occur in the posterior region just behind the major fold.

The radula is not evenly folded. Near the posterior margin of the preserved section (top of Figure *1*) the midsection of the radula is much more clearly observed. As the anterior portion (bottom of Figure *1*) is approached the radula narrows with the separation of central cusps becoming less obvious. This probably reflects the natural folding of the radular membrane, spread widest at the point of the anterior fold, then narrowing anteriorly towards the tip.

TOOTH STRUCTURE

On the basis of direct observations and comparative studies with radulae of extant mollusks, *Paleocadmus herdinae* is interpreted (Figure 25) as having thirteen radular elements in each row: one central tooth (C) with slight evidence of weak ectocones; two unicuspid, flanking laterals (L_1, L_2) on each side with laterally extended bases; two much larger, unicuspid, marginals on each side (M_1, M_2), the inner being smaller and more sharply curved; one inner marginal support plate (M_1P) that lies mostly under each outer marginal tooth and probably also served to lock the folded outer marginal into position when the latter was not erected; and, on the outer edge of each side, a small rectangular marginal plate (M_2P) that would serve to support the raised outer marginal during a cutting stroke. The evidence for reconstruction decisions on each tooth follows, together with a discussion of tooth details.

There are sixteen clear rows of impressions (Figure *1*), with partial traces for two additional anterior and seven more posterior rows. At the anterior end, lower part of Figure *1*, the rows are more compacted. The total width of the impression at the anterior is about 3.7 mm. At the posterior end, upper part of Figure *1*, the radula is expanded and the width of the impression is about 4.9 mm. Where the radula was expanded, information about the lateral teeth was far more available, whereas data on the marginals generally had to be taken from the more compacted areas.

The central tooth (C) seems to have been very weakly tricuspid. Vague lateral notches are visible in the impressions at J–K, 2–3, and I–J, 5. This area is shown at higher magnification in Figures *3* and *4*. These figures show the central with a deep and rounded upper side contour, but there is only slight evidence of widening more rapidly at the base. Hence the basic shape of the tooth is interpreted as continuing without marked widening to the anterior margin. Interpretation of the possible basal plate shape, with suggestion of the slight posterior extension of the basal plate, is taken from Figure *13*. A stray uncoated dust speck (white) surrounded by a dark halo serves to mark the position of the right first lateral. Just below this in the illustration is what we have interpreted as the basal plate remnants of the centrals. When viewed as stereo pairs, there is indication of a side shouldering as depicted in the reconstruction (Figure 25).

The first lateral teeth (L_1) also are shown most clearly in H–K, 4–8, of Figure *1*. The cusp shape is taken from these impressions, as is the pattern of the outer side of the cusp sweeping at an increasing angle towards the impression base. Where the cusp impression is deepest (I, 5, and H, 6.5) the lateral notch to the left is interpreted as part of the basal plate support rise to the cusp (see also G, 12). It is on this basis that the long posterior basal plate of the first lateral is shown. The angle of concretion splitting and the overlap by the inner marginal is such that we cannot predict, on its own merit, the exact length of the lateral extension in the 1st lateral. Basal plate impressions seen in Figure *13* do not show this area clearly. Just below the previously mentioned "dirt speck halo" a *possible* strong lateral extension is indicated, but it is not confirmed elsewhere, probably because of inner marginal overlap. The decision to show the very elongated lateral extension caused by an acceleration of the curvature shown in the lower left and far center right of Figure *3* is based partly on evidence concerning the 2nd lateral. On the left side of the radula, just above L, 3, of Figure *1*, the 2nd lateral appears as a separate cusped structure. Further down the same side, 7–12, it is seen as a small cusp with broadly curving base (center of Figure *8*). On the right side of the radula, particularly H, 4, then G, 7–11, of Figure *1*, much more is revealed. The 2nd lateral can be seen to slant very strongly and to be quite elongated laterally. In order to show the inner marginal support in Figure 25, we arbitrarily have shown only the tip of the cusp, and probably have overdeveloped the lateral slant of the 1st lateral tooth. We consider it reasonable for the 1st lateral to have less of a lateral extension than the 2nd lateral, but are uncertain as to what is the most probable configuration in *Paleocadmus*. On the basis of the lateral tooth structures in *Nautilus* (Figures *17–19*), the reconstructed 1st laterals (Figure 25)

probably are inaccurate, but they reflect the 2nd lateral structure.

Several features of the marginal teeth are noteworthy. Most obvious is their much larger size, sickle shape, with the inner (M_1) thicker and more sharply curved than the outer marginal (M_2). Nearly all of the impressions (Figures *1, 4, 7, 8, 12*) show a marked ridge. This translates as a groove on the upper marginal tooth surface. Higher magnification study of the groove (Figures *4, 7, 12*) shows that the groove is not "U"-shaped, but differs in contour on the two sides, as roughly indicated in Figure 25. The groove extends (Figure *12*) virtually to the tip of the marginal. Because of combined overlap by the outer marginal and the question of complications caused by the inner marginal support plate, we present no ideas concerning the basal shape of the inner marginal tooth. We simply show the curved shaft (Figure 25) disappearing below the tips of the outer marginals. There is a complicated set of impressions on the lower side (Figure *13*, upper fifth and lower half) that we believe represent a combination of the inner marginal support plate, lower part of the inner marginal, and basal area of the 2nd lateral tooth. We have not been able to make an independent reconstruction of this area from its own evidence. While the structures seen in *Nautilus* (Figures *18, 21*) seem fully consistent with the basal plate traces seen in *Paleocadmus* (Figure *13*), we consider the direct evidence insufficient for a reconstruction.

More evidence is available concerning the basal portions of the outer marginal (M_2). On the left side of the radula from L, 8, down to about K, 11 (Figure *1*), at least one corner of the outer marginal can be seen. The slight anterior flare and the abrupt truncation running virtually parallel to the midline of the radula is especially obvious at L, 8.5. More data are available from the lower side (Figure *5*). The upper impression of teeth from the left side of the radula clearly shows a more acute posterior flare and the continued truncated base, while the lower tooth impression in the same figure suggests that the base was curved, much as in *Nautilus* (Figure *21*, left). Hence the details of basic shape, grooving, and basal termination of the outer marginal in the reconstructed teeth are based on firmest evidence.

The outer marginal support plate (M_2P) is visible in upper surface relief in Figure *1*, particularly near D, 4.5, lower at C, 9–11, and then with less clarity at L, 9–11. The basic shape is short rectangular with slightly angled inner margin. There is a raised ridge located on the anterior side of center. On the lower side of the concretion, tips of the outer marginal support plate can be seen at the far left of Figure *5*. Please note the differential depth of the impression from top to bottom in the photograph.

Explanation of Figures *2* to *7*

Holotype of ***Paleocadmus herdinae*** Solem and Richardson, gen. nov., spec. nov.

Figure *2:* Folded section at middle area of radula, lower side impression X20.5

Figure *3:* Upper side impression, looking anteriorly from a low angle, I, 5-6 area in Figure *1*, impressions of two rows, central and flanking 1st lateral teeth, with tips of inner marginals visible upper left and lower right X93.5

Figure *4:* Upper side impression, area I-L, 5-7, showing central, weak 1st laterals, deep inner marginals, varying position of 2nd lateral tips (smaller impression above inner marginals), and partial outer marginal impressions, viewed at low angle from anterior X48.5

Figure *5:* Lower side impression of outer marginal tooth bases (left of center) and outer marginal plate (far left) from left side of radula, two rows represented X96

Figure *6:* Lower side impression of outer marginal plates (center) and outer marginal teeth bases from right side of radula, four rows represented X57

Figure *7:* Upper side impression from area D-G, 9-11.5 in Figure *1*, showing outer marginals (deeper impression on left), outer marginal plate (shallower impression on left), inner marginals (longer impression on right), 2nd laterals (shorter, upper impression on right), left side of radula X53

Explanation of Figures *8* to *13*

Holotype of ***Paleocadmus herdinae*** Solem and Richardson, gen. nov., spec. nov.

Figure *8:* Upper side impression from area H, 10 in Figure *1*, showing fragment of inner marginal tooth, under side of cusp tip and fracture through cusp (left of center), 2nd lateral cusp impressions (center), 1st lateral cusp impressions (far left), inner marginal (lower left and center), outer marginals (right) X84

Figure *9:* Detail of tooth fragment in Figure *8*, showing distortion of tooth under surface X262

Figure *10:* Fracture edge of tooth fragment X1105

Figure *11:* Surface of tooth fragment with bits of matrix (larger pebbles) and minor "pebbling" typical of radular surfaces X5150

Figure *12:* Outer marginals from area F, 3-4 of Figure *1*, showing position and length of groove (ridge in impression) on marginal teeth X40.5

Figure *13:* Lower side impression, anterior to left, posterior to right of photograph, basal plate of central just below largest haloed "dust speck" in center upper right area X26.5


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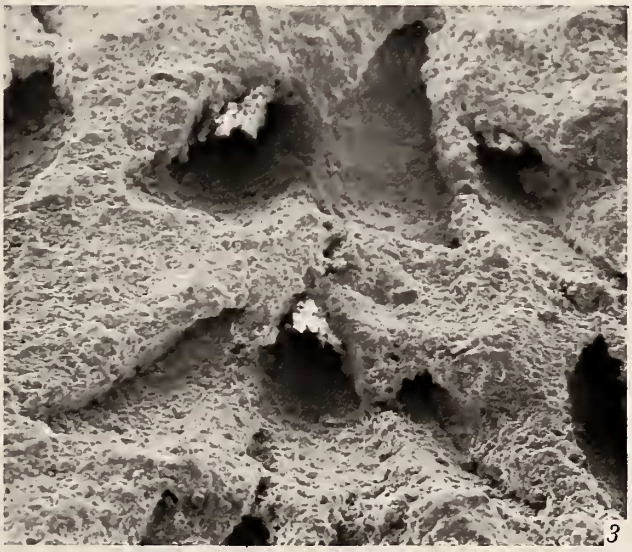
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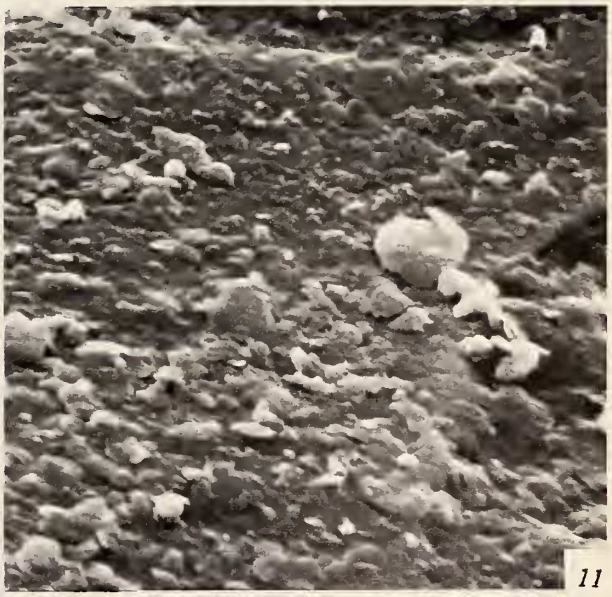
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